The Righting Response in Haliotids

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(1 Plate)

Haliotids are usually found subtidally. They are capable of swift movement over rock surfaces and occasionally may lose contact with the substrate. Wave and surge action may not be sufficient to right dislodged abalone and thus the adaptation of the righting response may be of significance. *Haliotis rufescens* Swainson, 1822 may become dislodged during storms from drift kelp on which it feeds (De Martini, personal communication) and frequently under these conditions the abalone gets washed ashore. The foot is tense and folded when in this state and the abalone is not capable of reattaching itself to the substrate. Cox (1962) has reported *H. rufescens* attached to kelp stipes; this however has not been seen by the author to occur in *H. kamtschatkana* Jonas, 1845 or *H. rufescens*.

The following experiment was conducted to determine whether an abalone would land inverted from a free fall in one meter of still water. The experimental animals were released 10 times from each of 10 different positions. When released from a series of vertical positions and from the inverted position, each of the 16 abalones, without exception, landed on its shell. Abalones released with the pedal sole at an angle of 45° to the substrate surface or from the upright position landed in the upright position in 11% and 17% of the cases, respectively. These abalones were free from shell epifauna excepting for some *Cliona* and encrusting coralline algae. This demonstrates that *Haliotis kamtschatkana* when detached from a surface will land more frequently in an inverted position; and thus the righting response may be of great importance.

The righting response in healthy abalones follows a consistent pattern and usually is completed within one minute. The 16 *Haliotis kamtschatkana* used in the experiments were collected from a depth of 6m at Salt Spring Island, British Columbia. These were placed upside down in trays in 12° C recycled sea water. When inverted the yellow pedal sole is covered by the lateral edges of the foot (which are black interrupted by spots and patches of pale yellow to orange) which overfold and meet medianly. The foot, after a period of time, stretches posteriorly over the lip of the shell and the posterior edge of the foot unfolds as the columellar muscle rotates slowly to one side. The posterior tip of the foot then comes in contact with the substrate, and as better contact with the substrate is made, the sole becomes more exposed. The columellar muscle then contracts with an accompanying rotation of the shell which causes the animal to right itself. The lateral edge of the foot then folds back to expose the full sole to the substrate surface. The animal then assumes its normal position. Seventeen individuals of *H. cracherodii* Leach, 1817, ranging in length from 14 to 82 mm, and 7 individuals of *H. rufescens*, ranging in length from 153 to 221 mm, all from Montana de Oro State Park, California were also observed to undergo the same pattern of activities in righting. The pedal sole of both of these species were darker. Occasionally individuals of *H. rufescens* were able to right themselves by extending the anterior portion of the foot over the edge of the shell.

None of the inverted abalones were able to right themselves on level sand, but all were able to move across the sand. The posterior end of the foot may be extended by as much as half the length of the shell; the foot initially twists violently, rocking the shell, but then by inserting the end of the foot in the sand it is able to lever the shell along. This movement is repeated until it comes in contact with a hard substrate when it is capable of righting the animal. *Haliotis cracherodii*, *H. kamtschatkana* and *H. rufescens* are all capable of travelling across sand in this manner. These 3 species were also observed to move across coarse sand with the sole in full contact with the substrate. The mean diameter of substrate particles over which *H. kamtschatkana* was capable of travelling ranged from 0.04 to 1.23 mm.

The righting response can be seen to be an advantage to inverted abalones. The yellow sole of an overturned

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Haliotis kamtschatkana is very noticeable underwater and so the lateral folding of the foot may assist to make the animal less conspicuous, particularly from *Scorpaenichthys marmoratus* Girard, a common fish predator of abalones (Cox, 1962).

Sand may not pose as much of a barrier as Cox (1962) originally thought. Abalones may be able to reach isolated outcrops of rocks, but in doing so may expose themselves to predation or dislodgement by water movement. Additional water movement may right inverted abalones or they may lever themselves to some hard substrate to which the sole can then attach. Unlevel sand, such as sand ripples, may facilitate righting in the absence of any hard substrate.

[ADDENDUM by the Editor:

In approximately 40 years of collecting along the coast of California I had many opportunities to observe various species of invertebrates in their natural habitats. Some unusual sights have been recorded in my memory, such as a small *Haliotis walallensis* Stearns, 1899 suspended from the stipe of *Laminaria andersoni,* about 40 cm above the water; this animal was swinging gently to and fro, activated by a slight breeze. Upon close-up examination, it was seen that the animal was holding on with only a small portion of its foot. A few years later, at Arena Cove, Mendocino County, I was able to photograph this very acrobatic species in the act of righting itself. However, in contrast to the "slow" process described above for *H. kamtschatkana,* this animal righted itself so rapidly that I was unable to obtain a satisfactory sequence of exposures in one righting effort, even though I took the pictures as rapidly as it was possible to cock and release the camera mechanism. The 4 pictures shown in Plate 1 thus were obtained in two series, a fact which will be evident on close examination. Nevertheless, I think that the pictures well illustrate the description given by Mr. Minchin above. I would estimate that "my" animal completed the righting effort in less than 15 seconds!]

Literature Cited

Cox, Keith W.
1962. California abalones, family Haliotidae. Fish. Bull. **118**; Calif. Dept. Fish and Game, Sacramento, Calif.

Explanation of Figures *1* to *4*

Four consecutive positions of *Haliotis walallensis* Stearns, 1899, in sequence, during righting response. However, the transition from position 1 to position 3 was so rapid that a second righting response had to be evoked in order to obtain a picture of position 2. The transition from position 1 to position 4 required less than 15 seconds. From Kodachrome color slides taken June 20, 1970 at Arena Cove, Mendocino County, California by R. Stohler